

A NEW EARLY DEVONIAN GALEASPID FROM BAC THAI PROVINCE, VIETNAM

by P. JANVIER, TÔNG-DZUY THANH and TA-HOA PHUONG

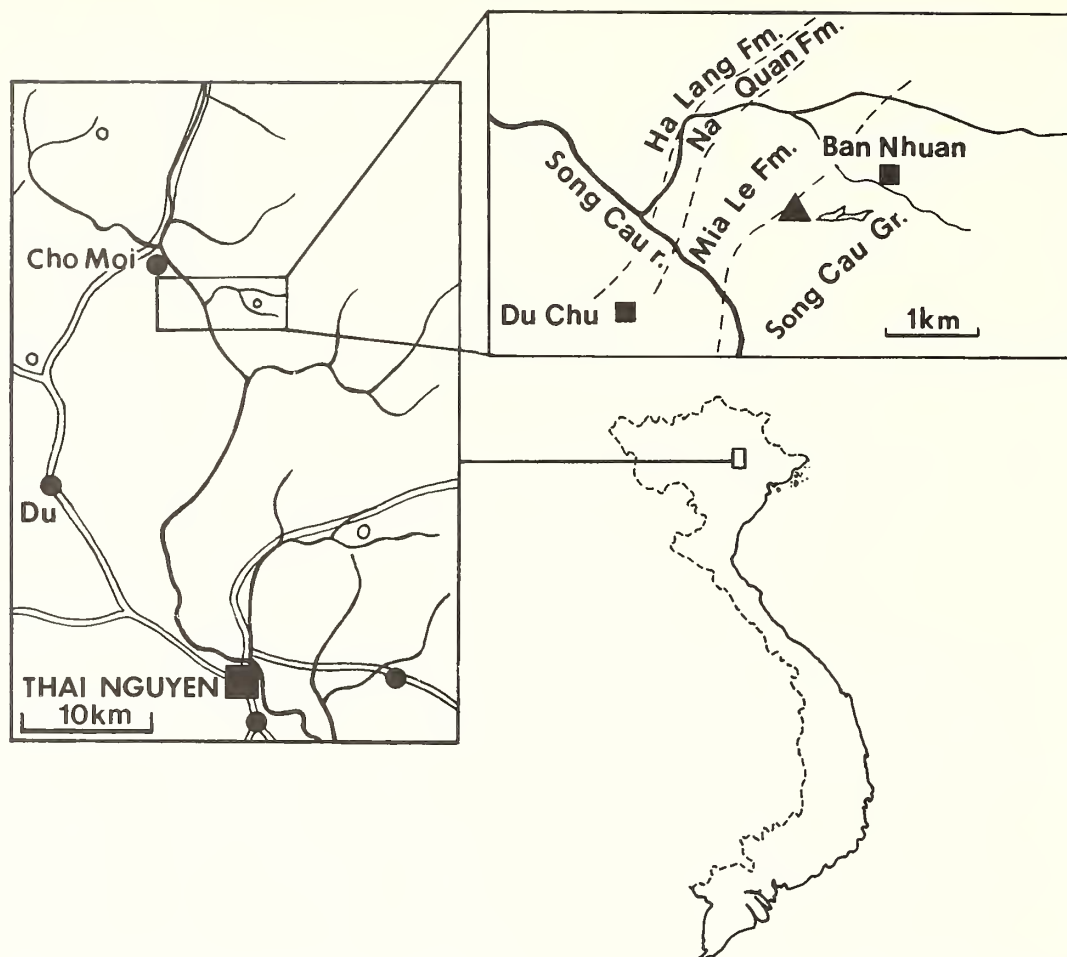
ABSTRACT. A new large galeaspid, *Bannhuanaspis vukhuci* gen. et sp. nov., is described from the top part of the Si Ka Formation or the base of the Bac Bun Formation (Early Devonian, Late Lochkovian or Early Pragian) in the Phu Luong District, Bac Thai Province, northern Vietnam. The overall shape of its head shield is suggestive of the 'Polybranchiaspidiformes', but this morphology is regarded as a primitive feature for the Galeaspida. Its transversely elongated median dorsal opening, broad posterior margin of head shield and posterolaterally directed main lateral-line are also regarded as primitive galeaspid characteristics. However, it shares with the 'Polybranchiaspidiformes' and Huananaspidiformes a large number of gill openings, and with the Galeaspidiformes very short and rounded cornual processes.

THE Galeaspida, a group of Silurian and Devonian jawless vertebrates endemic to China and Vietnam, were first described by Y. H. Liu (1965), but it is now clear that the small fragments of exoskeleton referred to by Mansuy (1915, pl. 1, figs 2–5) as 'ostracoderme indéterminé', from the Si Ka Formation of Northern Vietnam (Lung Co-Si Ka section) is the earliest known record of this group. Y. H. Liu (1975) restricted the name Galeaspida to the genus *Galeaspis*, and considered this group as allied to the Osteostraci, within the Cephalaspidomorphi. The other jawless vertebrate genus he recorded from the Devonian of China, *Polybranchiaspis*, was thus placed in a group of its own, the Polybranchiaspida, which he regarded as related to the Heterostraci (Y. H. Liu 1975). Halstead Tarlo (1967) lumped the two groups into the Galeaspida, and he was later followed by Janvier (1975) and all subsequent writers. *Galeaspis* turned out to be preoccupied and was replaced by *Eugaleaspis* (Y. H. Liu 1980), but the change of Galeaspida into Eugaleaspida or Galeaspidiformes into Eugaleaspidiformes (Y. H. Liu 1980) was unnecessary, since the rules of nomenclature do not apply to taxa above the family-group level, and since these higher taxa were not preoccupied. Therefore, the names Galeaspida and Galeaspidiformes Liu are retained here.

Besides the fragments collected by J. Deprat around 1910, and described by Mansuy in 1915, the first evidence of determinable galeaspids from Vietnam dates back to 1973, when three incomplete head shields collected by Ta-Thanh Trung in the Si Ka Formation of Tong Vai, Quan Ba district, Ha Giang Province, were sent to China for identification. These have been determined as *Polybranchiaspis* 'nov. sp.', close to *P. liaojaoshanensis* Liu (Ta-Thanh 1978; Pan Jiang, unpublished report to the Institute of Geology and Mineral Resources, Hanoi, 1978). Tông-Dzuy and Janvier (1987), on the basis of photographs, suggested that they might rather belong to *P. gracilis* Cao, 1986, which, however, may well be a mere individual variation of *P. liaojaoshanensis*. The three specimens, quoted as lost by Tông-Dzuy and Janvier (1987), have now been found to be deposited in the Geological Institute of the Academia Sinica, Beijing.

Fragments, scales, or incomplete shields of galeaspids have also been recorded from more southerly localities in Vietnam, namely in Trang Xa (Bac Thai Province: Tông-Dzuy and Janvier 1987), and Dong Mo (Lang Son Province: Tông-Dzuy and Janvier, 1990).

The present description of a new and unusually large galeaspid from Vietnam is based on material collected in 1991 in the locality of Ban Nhuan, Phu Luong district, Bac Thai Province. The specimen belongs to the collection of the Department of Geology of the University of Hanoi (UHDG, VND 50-52).



TEXT-FIG. 1. Locality map, showing the distribution of the Song Cau Group and the Mia Le, Na Quan and Ha Lang Formations across the Song Cau river. The galeaspid locality near Ban Nhuan is indicated by a black triangle.

GEOLOGICAL SETTING

Early Devonian vertebrate faunas of Vietnam occur exclusively in the Si Ka and Bac Bun Formation of the Bac Bo (formerly the Tonkin), both united as the Song Cau Group (Tông-Dzuy 1980). Their age was first believed to be Eifelian (Long 1967), but recent re-examination of the associated or overlying invertebrate faunas (in particular brachiopods and corals) has shown that they were rather Late Lochkovian or Early Pragian in age (Tông-Dzuy 1980; Tông-Dzuy *et al.* 1986; Tông-Dzuy and Janvier 1990). This new dating is also supported by faunal comparisons with the Early Devonian vertebrate-bearing localities of southern China, in particular Qujing, Yunnan, and Liujing, Guangxi. The fish-bearing parts of the Si Ka and Bac Bun Formations could thus be correlated with the lower part of the Cuifengshan Formation of Yunnan or the uppermost part of the Lianhuashan Formation of Guangxi (Pan and Dineley 1988), that is the 'Siegenian' (Upper Lochkovian–Lower Pragian) in the sense of S. T. Wang (1991). Previous work (Pham-Dinh 1967), as well as field investigations carried out since 1985 by the present authors, suggests that there are

several fish horizons in the Si Ka and Bac Bun Formations, and that, despite similarities in the higher taxonomic composition, differences at the specific or generic level may be due to slight differences in age rather than to differences in environmental conditions (Tông-Dzuy and Janvier, submitted). The new galeaspid described here from Ban Nhuan, for example, has never been observed in any of the major fish localities of the Bac Bo (Tranx Xa, Dong Mo), even in the form of exoskeletal fragments.

The locality of Ban Nhuan is situated 18 km north east of the town of Du, in the Phu Luong District, approximately 30 km north of Thai Nguyen, on the southern margin of a large Palaeozoic anticlinorium (Text-fig. 1). There, the Si Ka and overlying Bac Bun Formation (Song Cau Group) outcrop at the base of the hills, their top being generally made up of the limestone of the Mia Le and Na Quan Formations and the siliceous shales of the Ha Lang Formation. All these formations are intersected by the Song Cau river. The best exposures occur along the path leading from the Song Cau river to Ban Nhuan, about one kilometre before arriving at the village. There, several bone-beds are clearly visible within the massive dolomitic sandstone of the top of the Si Ka Formation. The large galeaspids described herein occur in a very fine-grained dolomitic sandstone at the top of the formation, probably just below the uppermost bone-bed. This type of sediment corresponds to a low-energy environment which permitted the preservation of the extremely thin and fragile galeaspid exoskeleton. Fragments of exoskeleton with a similar structure occur also in the bone-beds, in association with numerous fragments of plates and scales of yunnanolepid antiarchs and youngolepid sarcopterygians. From the lithology, these fish-bearing beds can be placed near the boundary between the clastic Si Ka Formation and the dolomitic Bac Bun Formation.

These large galeaspid shields are associated with some antiarch plate fragments, one of which could be determined as an anterior ventrolateral plate of *Yunnanolepis* sp.

SYSTEMATIC PALAEONTOLOGY

Class GALEASPIDA Liu, 1965
Order and Family undetermined
Genus BANNHUANASPIS gen. nov.

Derivation of name. After Ban Nhuan, the type locality of the type species.

Type species. *Bannhuanaspis vukhuci* sp. nov.

Diagnosis. As for the type species

Bannhuanaspis vukhuci sp. nov.

Text-figs 2–6

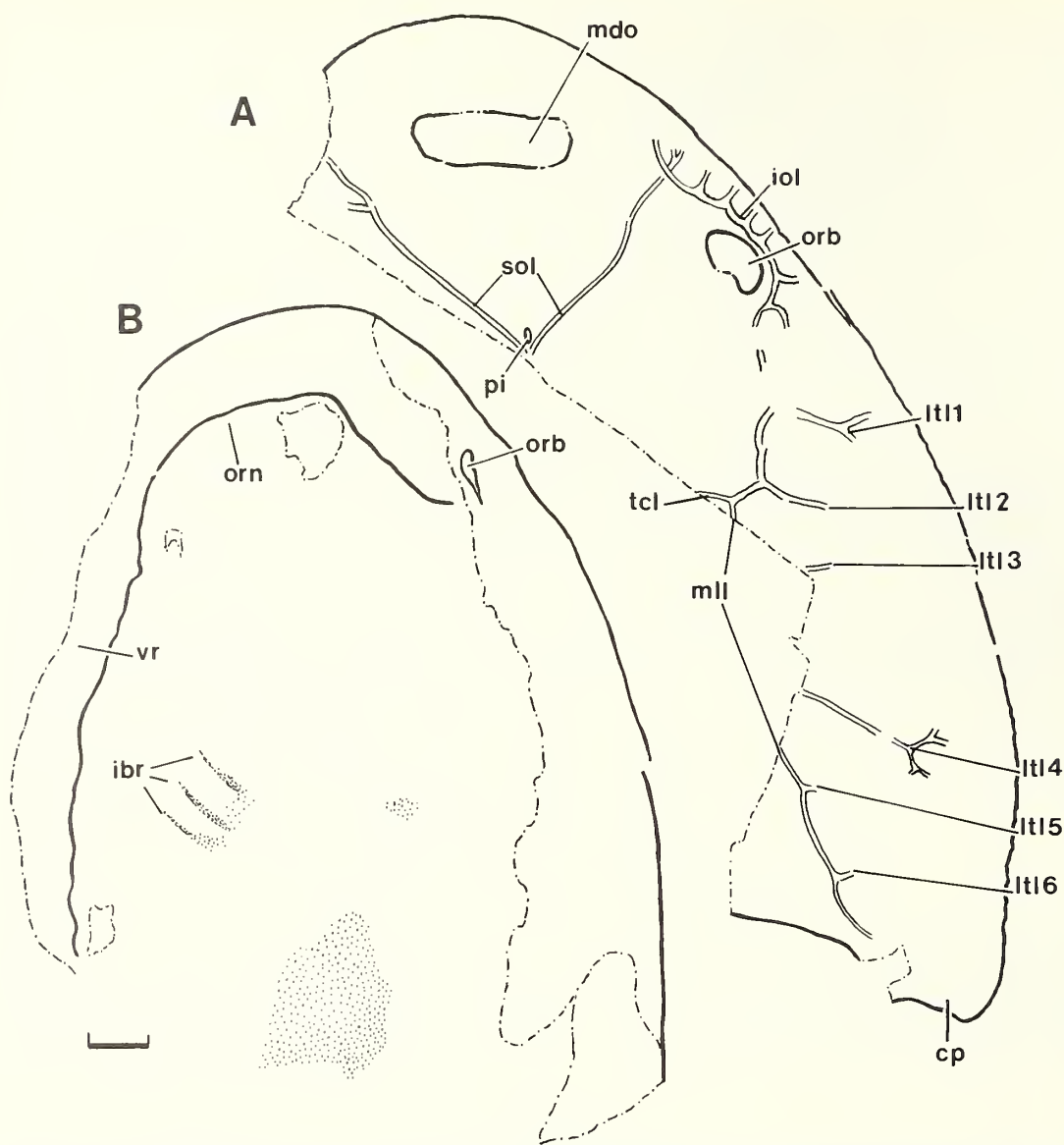
Derivation of name. The species is dedicated to Dr Dang Vu Khuc, Geological Museum, Hanoi.

Diagnosis. A very large polybranchiaspidid-like galeaspid, with orbits situated close to the shield margin and a transversely elongated median dorsal opening. The maximum breadth of the shield is situated in its rearmost part.

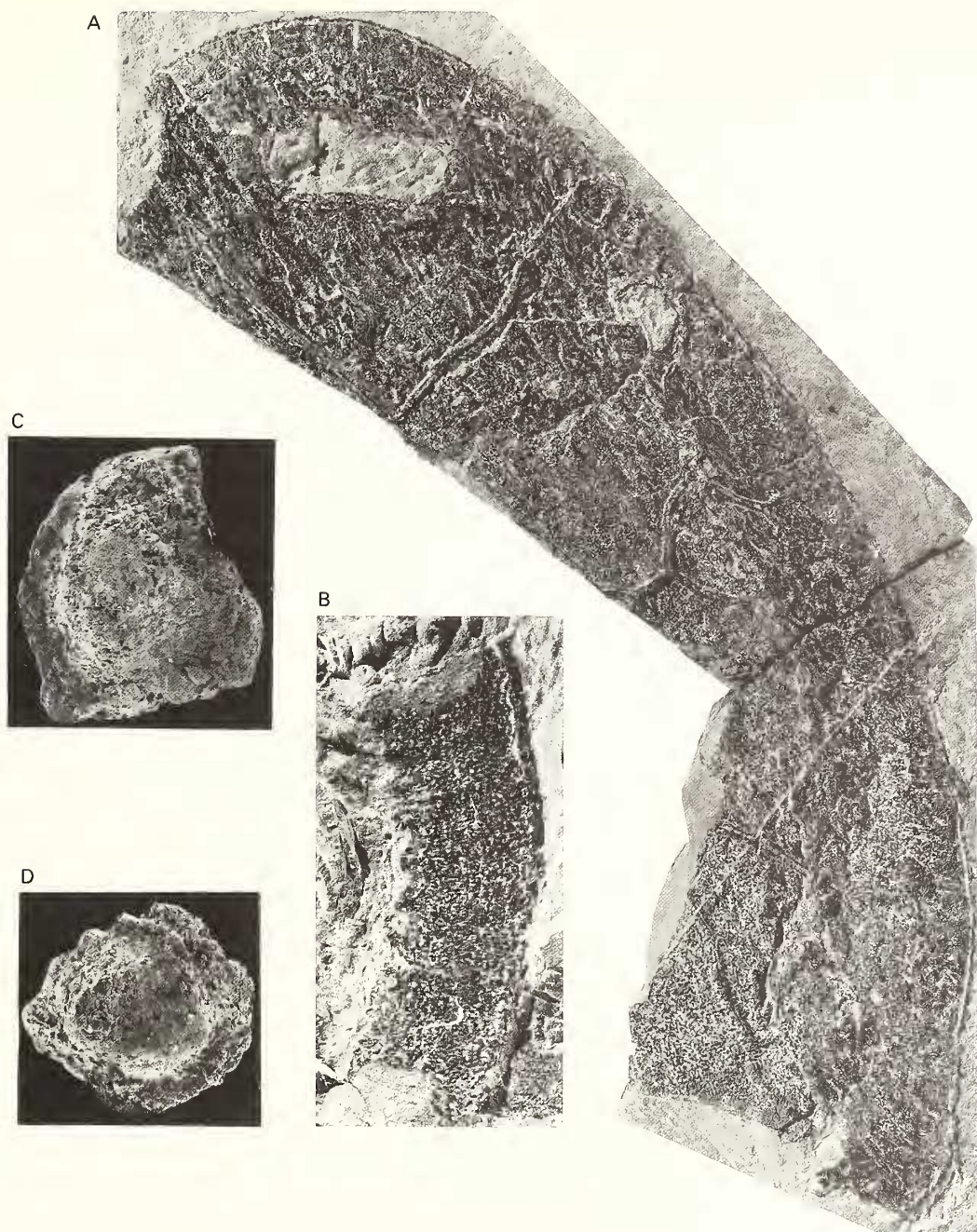
Holotype. An incomplete head shield (University of Hanoi, Department of Geology, VND 50; Text-figs 2, 3A), part and counterpart.

Type locality. Ban Nhuan, North East of Du, Phu Luong District, Bac Thai Province, Vietnam (Text-fig. 1)

Type horizon. Uppermost part of the Si Ka Formation or lowermost part of the Bac Bun Formation, Lower Devonian, Late Lochkovian to Early Pragian.



TEXT-FIG. 2. *Bannhuanaspis vukhuci* gen. et sp. nov. Lower Devonian (Late Lochkovian to Early Pragian), top part of Si Ka Formation or base of the Bac Bun Formation; Ban Nhuan, Phu Luong district, Bac Thai Province, Vietnam; holotype (VND 50); interpretive scheme of head shield. A, dorsal part of incomplete dermal head shield in ventral view, showing the canals of the sensory-line system. B, counterpart of the latter specimen, showing part of the marginal region and ventral rim of the dermal head shield in dorsal view; traces of perichondral bone from endoskeleton dotted. Scale bar = 10 mm. Abbreviations: cp, cornual process; ibr, trace of interbranchial ridges; iol, infraorbital portion of main lateral line; ltl 1-6, lateral transverse lines; mdo, median dorsal opening; mll, main lateral-line; orb, orbit; orn, oral notch; pi, pineal foramen; sol, supraorbital line; tcl, transverse commissural line.

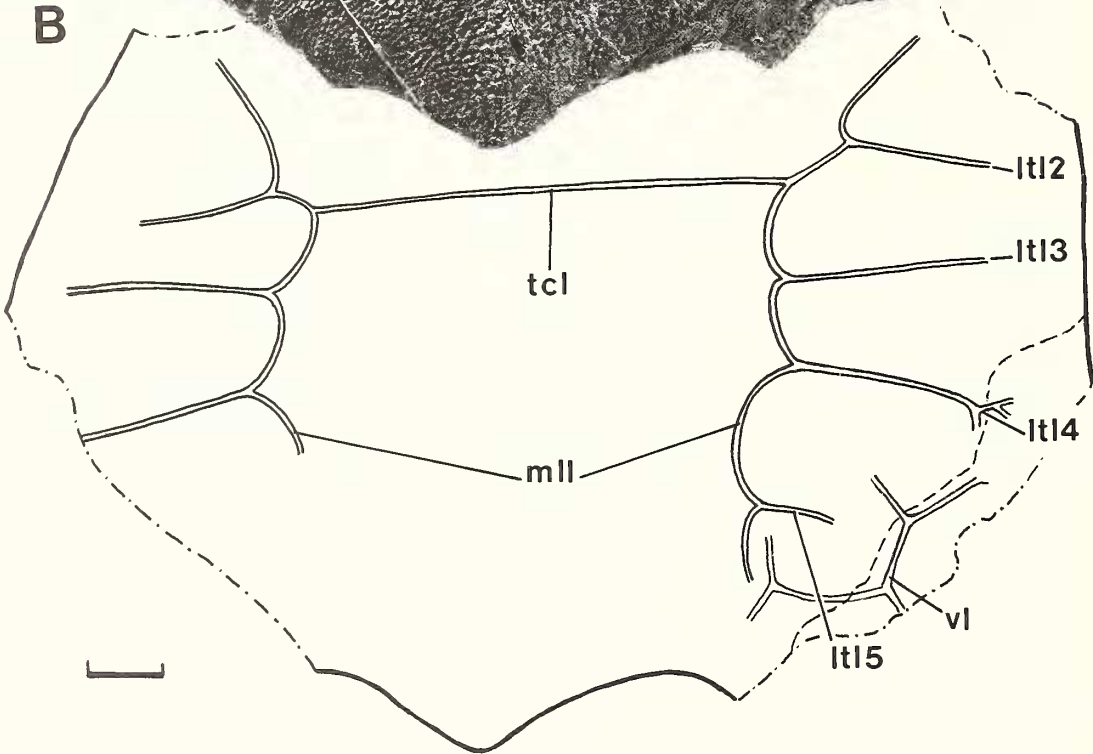


TEXT-FIG. 3. *Bamhuanaspis vukhuci* gen. et sp. nov. Lower Devonian (Late Lochkovian to Early Pragian), top part of Si Ka Formation or base of the Bac Bun Formation; Ban Nhuan, Phu Luong District, Bac Thai Province, Vietnam. A, Incomplete head shield (holotype, VND 50), exoskeleton in ventral view (for interpretation see Text-fig. 2A), $\times 1$. B, fragment of ventral rim of head shield (VND 52), showing branchial notches, (for interpretation see Text-fig. 5A), $\times 1$. C–D, isolated scales of the body squamation, associated with the holotype; scanning electron micrographs of the external surface, $\times 50$.

A



B



Referred material. Posterior median dorsal part of the head shield (VND 51, Text-figs 4, 5A), isolated fragment of ventral rim of the shield (VND 52, Text-fig. 3B, Text-fig. 5A) isolated scales in association with the latter specimens (Text-fig. 3C–D).

Remarks. *Bannhuanaspis vukhuci* is one of the largest known galeaspid, together with the primitive Silurian genus *Hanyangaspis* (N. Z. Wang 1986), *Dongfangaspis major* (Y. H. Liu 1975) and *Antiquisagittaspis* (Y. H. Liu 1985). Its closest overall resemblance is to *Polybranchiaspis*, from which it differs however by the more lateral position of the orbits, the more posteriorly placed and more transversely elongated median dorsal opening, the broader posterior limit of the head shield, and its larger size. Although the sensory-line pattern is broadly similar to that of *Polybranchiaspis*, it differs from the latter in that the posterior part of the main lateral-line is posterolaterally – and not posteriorly – directed (*mll*, Text-figs 2A, 4B). This feature was previously known only in *Hanyangaspis* and *Xiushuiaspis* (N. Z. Wang 1991).

The question of the systematic position of *Bannhuanaspis* can only be answered in the context of the question of the monophyly of the ‘Polybranchiaspidiformes’, which will be briefly discussed below.

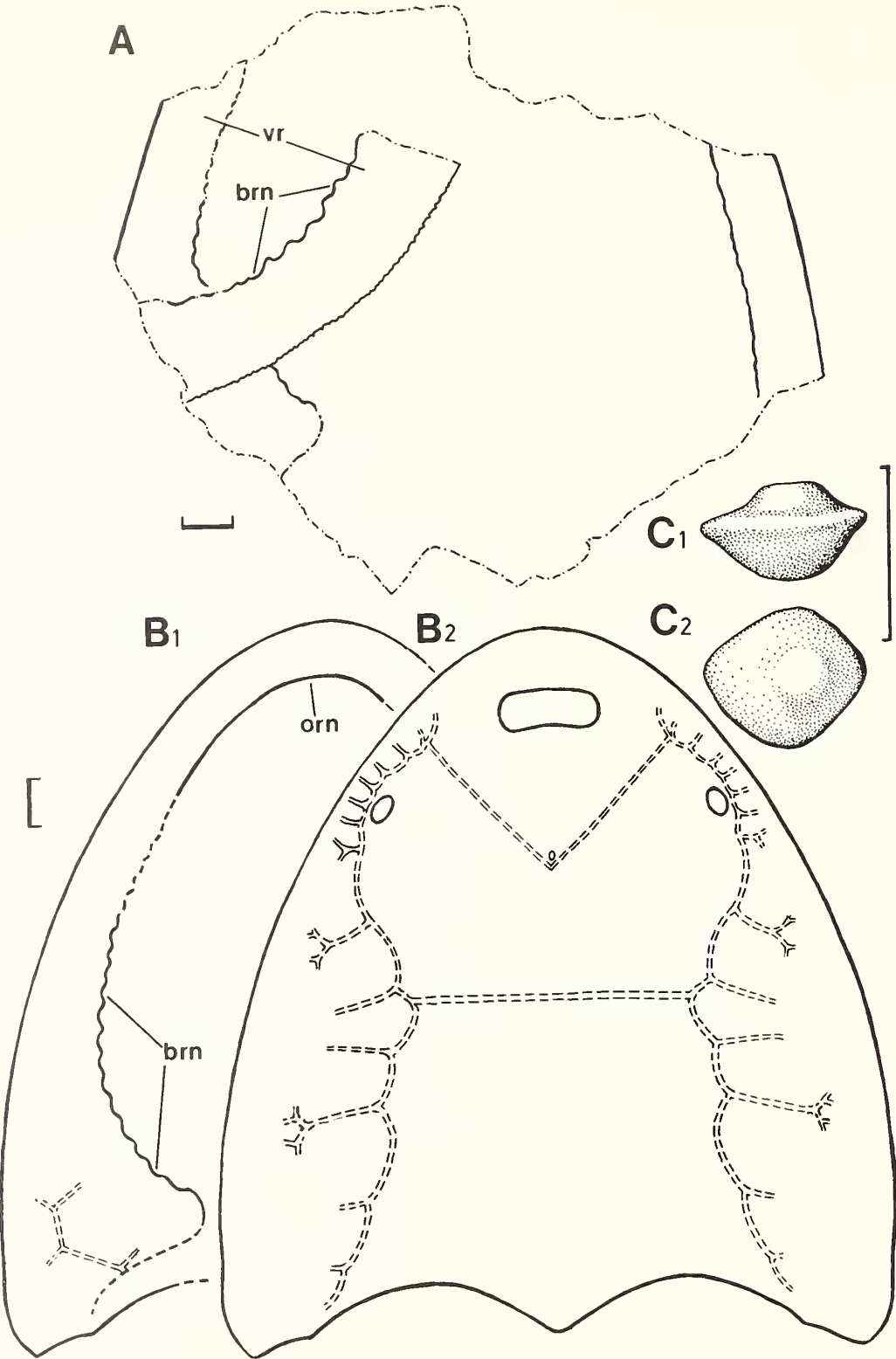
Description. The holotype VND 50 is a slightly distorted and incomplete head shield, the dorsal aspect of which is known from the ventral surface of the dorsal exoskeleton (Text-figs 2A, 3A). The canals of the sensory-line system, which, in galeaspid, lie against the basal surface of the exoskeleton (Janvier 1990), are thus clearly visible. The median dorsal opening (*mdo*, Text-fig. 2A) is transversely elongated, roughly rectangular in shape, with rounded angles, and situated relatively far behind the anterior margin of the shield. One of the orbits is visible on the left side, although slightly distorted by crushing (*orb*, Text-fig. 2A). A pineal foramen is present (*pi*, Text-fig. 2A).

The posterior median dorsal shield fragment VND 51 (Text-figs 4, 5A), which was used for completing the reconstruction in Text-figure 5B, exhibits the dorsal surface of the exoskeleton. Therefore, no sensory-line canal is visible in external aspect, beside a minute series of slits by which these canals open to the exterior (Text-fig. 6). The pattern of these canals in this specimen could, however, be traced on a radiograph (Text-fig. 4B). This specimen, which is similar in size to the holotype, and which was found in the same block, could be assembled to the latter, thanks to the position of the posterior margin of the shield and of the transverse commissural sensory-line canal (*tcl*, Text-figs 2A, 4B). Clearly, there is only one commissural canal, a condition which is regarded as a synapomorphy of all the galeaspid, apart from *Dayongaspis*, *Xiushuiaspis* and *Hanyangaspis* (Janvier 1984; N. Z. Wang 1991). There are probably six lateral transverse sensory-lines (*ltl* 1–6, Text-figs 2A, 4B). The infraorbital portion of the main lateral-line (*iol*, Text-fig. 2A) sends off numerous side-branches toward the shield margin, and is connected anteriorly with the distal part of the supra-orbital line (*sol*, Text-fig. 2A). Although no sensory-line canal has ever been reported in the ventral exoskeleton of the Chinese galeaspid, this specimen clearly shows such a canal extending on the lateral part of the dermal postbranchial bar and of the ventral rim (*vl*, Text-figs 4B, 5B1). It displays a zig-zag pattern which differs from that of the dorsal lateral-line canals.

The posterior margin of the shield is remarkably broad, with only shallow embayments on either side of a median dorsal process. There is no distinct median dorsal crest, but a slight median elevation in the rearmost part of the shield. Laterally, the posterior margin of the shield is produced into a slight lobe, which may have extended beyond the level of the body and may represent an incipient cornual process (*cp*, Text-fig. 2A).

The ventral surface of the head shield is known from the counterpart of the holotype, which displays a slight oral notch (*orn*, Text-figs 2B, 5B), and from the ventral side of isolated median shield fragment, which shows part of the ventral rim of the oralbranchial fenestra (*vr*, Text-fig. 5A). With this specimen, there is also an isolated portion of ventral rim detached from another shield (Text-figs 3B, 5A). These latter two specimens clearly show the series of branchial notches (*brn*, Text-fig. 5A–B), which are quite numerous and suggest thus a condition comparable to that in *Polybranchiaspis* or *Duyunolepis*, though the precise number of these notches

TEXT-FIG. 4. *Bannhuanaspis vukhuci* gen. et sp. nov. Posterior median part of head shield (VND 51), same locality and level as the holotype. A, specimen in dorsal view, showing the external aspect of the exoskeleton, and some sensory-line canals of the ventral exoskeleton on the right side. B, distribution of the sensory-line canals, based on a radiograph of the specimen. Scale bar = 10 mm. Abbreviations: *ltl* 2–5, lateral transverse lines; *mll*, main lateral-line; *tcl*, transverse commissural line; *vl*, ventral sensory-lines.



remains unknown (Text-fig. 5B1). The dermal postbranchial bar does not seem to be complete (Text-fig. 5A, B1). The dermal covering of the oralbranchial fenestra is unknown.

Some slight traces of perichondral bone from the endoskeleton are visible in the counterpart of the holotype, within the sediment which fills the oralbranchial fenestra. A series of transverse strands of perichondral bone may represent traces of the interbranchial ridges of the roof of the oralbranchial chamber (*ibr*, Text-fig. 2B).

The organization of the exoskeleton is quite similar to that described in *Polybranchiaspis* sp. by Janvier (1990) and N. Z. Wang (1991). It consists of loosely assembled, minute dermal units, each of which bears a single tubercle covered with a shiny hard tissue (possibly an enameloid). The exoskeleton is completely recrystallized and its microstructure cannot be studied.

Numerous scales occur in the sediment in association with the shields, sometimes arranged into parallel series which suggest that they retain their original position, as described by S. F. Liu (1983) in *Eugaleaspis*. All the scales are minute rounded units (Text-figs 3C–D, 5D–E), quite similar in shape and structure to the individual units of the dermal head shield. They have no pulp cavity and bear a single boss, or tubercle (Text-fig. 5C) covered with a shiny hard tissue (Text-fig. 3D).

DISCUSSION

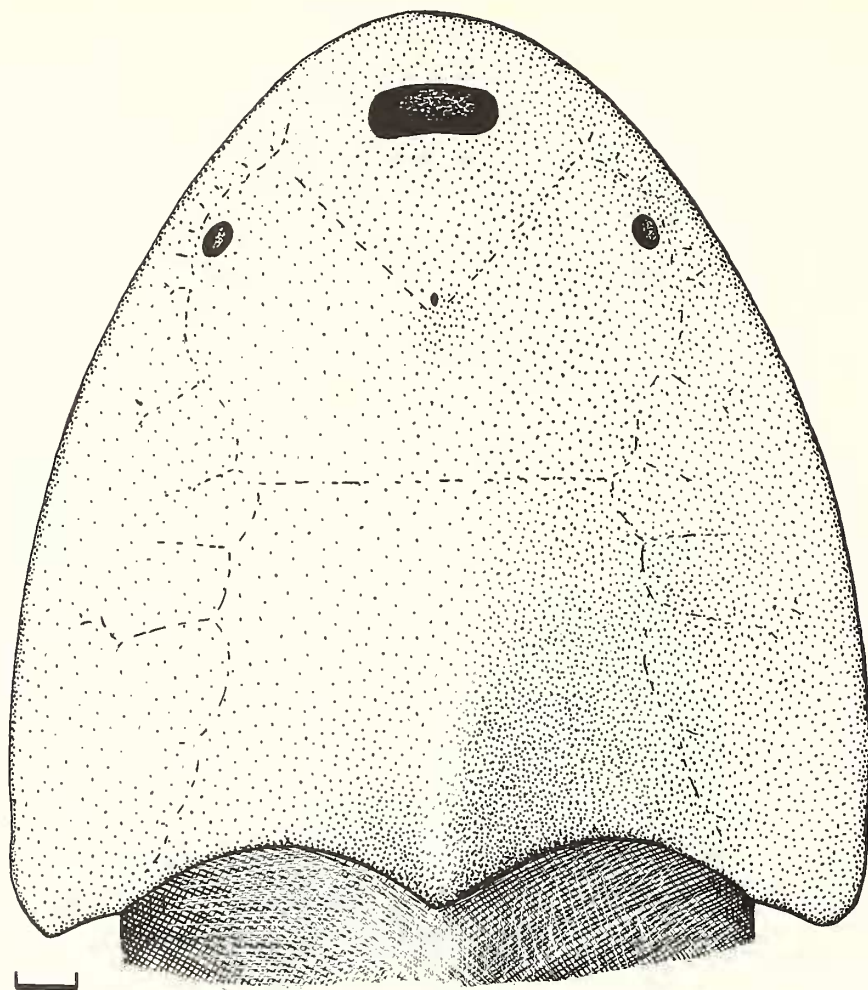
The phylogenetic interrelationships of the Galeaspida have been briefly discussed by Janvier (1984), S. F. Liu (1986) and in more detail by N. Z. Wang (1991). The first question that arises in this connection is that of the sister-group of the Galeaspida, which may serve as an out-group to evaluate character-state polarities. The Galeaspida have been regarded as the sister group of the Osteostraci (Janvier 1975; Halstead 1982; Young 1991), the Osteostraci + Gnathostomata (Forey 1984; Janvier 1984; Maisey 1986), the Gnathostomata alone (N. Z. Wang 1991), or also in a trichotomy with the Osteostraci and Gnathostomata (Young 1991, as a second possibility).

The current classification of the Galeaspida comprises four orders: the Hanyangaspidida: (*Hanyangaspis*, *Xiushuiaspis*, *Dayongaspis*); the Polybranchiaspidiformes (*Polybranchiaspis*, *Dongfangaspis*, *Diandongaspis*, *Laxaspis*, *Damaspis*, *Siyingia*, *Cyclodiscaspis*, *Duyunolepis*, *Paraduyunaspis*, *Neoduyunaspis*); the Huananaspisidiformes (*Huananaspis*, *Asiaspis*, *Nanpanaspis*, *Lungmenshanaspis*, *Sanqiaspis*, *Sanchaspis*, *Wumengshanaspis*, *Sinoszechuanaspis*); and the Galeaspisidiformes (*Eugaleaspis*, *Sinogaleaspis*, *Yunnanogaleaspis*, *Meishanaspis*, *Tridensaspis*). In addition, there are some genera *incertae sedis*, based on too poorly preserved material (*Antiquisagittaspis*, *Kwangnanaspis*, *Qingmenaspis*).

The Hanyangaspidida and the Polybranchiaspidiformes are most probably paraphyletic. *Hanyangaspis* is now regarded as being the sister-group of all other Galeaspida (Janvier 1984). The Polybranchiaspidiformes cannot be defined on the basis of a unique derived characteristic.

The number of characters available to reconstruct galeaspid phylogeny is quite limited because of the generally poor preservation of the specimens. They are: (1) the shape and position of the median dorsal opening, (2) the position of the orbits, (3) the overall shape and proportions of the head shield, (4) the pattern of the sensory-line canals, and (5) the number of gill openings or corresponding gill compartments. Features of the internal anatomy and ventral dermal covering of the oralbranchial chamber are so rarely preserved, and apparently so homogeneous throughout the entire group (apart from the more or less sinuous course of the dorsal jugular vein or the extension of the dorsal wall of the abdominal cavity), that they are not considered at the moment to be useful for unravelling the relationships within the Galeaspida. However, there are probably more characters to be found in the ventral dermal covering of the head shield, but this remains poorly known.

TEXT-FIG. 5. *Bannhuanaspis vukhuci* gen. et sp. nov. A, drawing of the ventral side of the specimen in Text-figure 2, showing part of the ventral rim of the dermal head shield, as well as a fragment of the ventral rim of a presumably different specimen of the same species (VND 52). B, reconstruction of dermal head shield in ventral (B1) and dorsal (B2) aspect, with the pattern of the sensory-line canals reconstructed on the basis of the specimens in Text-figures 2 and 4. C, reconstruction of an isolated body scale in lateral (C1) and external (C2) view. Scale bar: A–B = 10 mm, C = 1 mm. Abbreviations: *brn*, branchial notches; *orn*, oral notch; *vr*, ventral rim.



TEXT-FIG. 6. *Bannhuanaspis vukhuci* gen. et sp. nov., reconstruction of the head and anterior part of trunk squamation in dorsal view. Scale bar = 10 mm.

Out-group comparison does not tell us much of the plesiomorphic state of most of these characters. The median dorsal opening is apparently unique to the Galeaspida. Although Janvier (1981, 1984) regarded it as homologous to the nasopharyngeal duct of hagfishes and to the presumed prenasal sinus of the Heterostraci. In this case, the closer this median dorsal opening is to the anterior shield margin, the more plesiomorphic it is. *Hanyangaspis*, in which this opening is almost terminal in position, would thus show the most generalized condition for the Galeaspida. Moreover, a transversely elongated opening (as in *Hanyangaspis*) would be plesiomorphic relatively to an oval, elliptic, rounded, heart- or slit-shaped opening, if evaluated by reference to the Heterostraci. Conversely, the rounded opening of *Dayongaspis* would be plesiomorphic if assessed by reference to hagfishes.

The generalized position of the eyes for the vertebrates is a lateral position, and the dorsally placed eyes of some galeaspids is thus presumably derived. Therefore, the more laterally placed the eyes are, the more plesiomorphic is the condition. This condition is again met with in *Hanyangaspis* and possibly in a few other galeaspid taxa (*Cyclodiscaspis*, *Sanqiaspis*, *Huananaspis*).

The overall shape and proportions of the head shield are quite diverse in galeaspids, and the

elongated shape of the head shield of *Hanyangaspis* recalls strikingly that of the head in many thelodonts (e.g. *Turinia*), a group of supposedly jawless vertebrates regarded as an ensemble of generalized primitive vertebrates. This might be an indication that the morphology of *Hanyangaspis* is closest to the plesiomorphic state for the galeaspids. The 'Polybranchiaspidiformes' would thus be slightly derived, relatively to *Hanyangaspis*, in having a somewhat narrower and more oval shield, some of them having, in addition, a deep posterior median embayment. In this respect, the shield shape of *Bannhuanaspis*, with its wide and shallow posterior embayment, would be closer to that of *Hanyangaspis* than to that of other 'Polybranchiaspidiformes'.

The pattern of the sensory-line canals is unique to the Galeaspida, with a typically festooned pattern of the main lateral-line, but the supraorbital lines, meeting behind the pineal foramen, may be regarded as a generalized vertebrate feature. Yet, these lines seem to be lacking in *Hanyangaspis*, *Dayongaspis* and *Xiushuiaspis* (see, however, contradictory interpretations in Y. H. Liu 1986). The sensory-line canal pattern is quite homogeneous in all galeaspids, yet with minor differences, such as the connection between the supraorbital and medial longitudinal lateral lines in the Eugaleaspidoformes (Y. H. Liu 1986), or the presence of two transverse commissural lines in *Dayongaspis*, *Xiushuiaspis* and *Hanyangaspis*, a feature regarded by Janvier (1984) as plesiomorphic and N. Z. Wang (1991) as apomorphic. In fact, several transverse commissural canals occur in primitive heterostracans, osteostracans and gnathostomes (Y. H. Liu 1986). The presence of a single commissural canal in all galeaspids except these three genera may thus be regarded as apomorphic. In some galeaspids, the distal end of the lateral transverse canals, branching off laterally from the main lateral-line canal, seems to display a peculiar star-shaped pattern which may be unique to a monophyletic group within the 'Polybranchiaspidiformes', and which would thus include *Laxaspis*, *Diandongaspis*, *Cyclodiscaspis*, and *Dongfangaspis*. Such a structure has not been observed in *Bannhuanaspis*, although the distal end of the transverse canals is branched (Text-fig. 2A).

The number of external branchial openings or branchial compartments varies from seven to ten in most Silurian and Devonian jawless vertebrates (Heterostraci, Osteostraci, Thelodonti), except in the Anaspida, where it may reach fifteen or more. In the Galeaspida, *Hanyangaspis* and *Xiushuiaspis* possess only seven branchial openings or branchial compartments (N. Z. Wang 1986, 1991). In most other galeaspids, except the Galeaspidoformes (*Sinogaleaspis*, *Yunnanogaleaspis*, *Eugaleaspis* and possibly *Tridensaspis*), the number of gill openings and branchial compartments is very high (up to twenty-four pairs in *Paraduyunaspis*). The phylogenies of the Galeaspida proposed by Janvier (1984) and N. Z. Wang (1991) both imply the paraphyly of the 'Polybranchiaspidiformes' and a reversal to a low number of branchial compartments in the Galeaspidoformes (six or seven: Y. H. Liu 1975; Pan and Wang 1980). In both phylogenies, the sister-group of the Galeaspidoformes is the Huananaspidoformes, which are characterized by a rostral process, but clearly possess a much higher number of branchial compartments (Y. H. Liu 1975; Pan and Wang 1981). The two groups share cornual processes, that is, lateral expansions of the lateral shield margin. This supposedly reversed condition of the Galeaspidoformes with respect to the number of gill openings is in contradiction with their early occurrence (Late Wenlockian), together with rather plesiomorphic galeaspid genera such as *Xiushuiaspis*. It would be premature, at this level of knowledge of galeaspid anatomy, to produce one more phylogeny of the Galeaspida, and the remarks above are only aimed at showing that, if one considers *Hanyangaspis*, *Xiushuiaspis* or *Dayongaspis* (or all three: see N. Z. Wang 1991) as the sister-group of all other galeaspids, one may recognize among the latter two major monophyletic groups: the Huananaspidoformes, possessing a rostral process, and the Galeaspidoformes, possessing a short head shield and a slit-shaped median dorsal opening. In contrast, the 'Polybranchiaspidiformes' cannot be defined on the basis of a unique character, their oval shield shape being most probably plesiomorphic, as it occurs also in *Xiushuiaspis*, and they have a large number of gill openings, like the Huananaspidoformes. *Bannhuanaspis* shares with the Galeaspidoformes a posteriorly broad head shield with short cornual processes, and with the 'Polybranchiaspidiformes' and Huananaspidoformes a large number of gill openings. The transversely (yet moderately) elongated median dorsal opening is a general galeaspid feature, variously modified within this group. Although *Bannhuanaspis* possesses a single transverse

commissural canal which puts it among 'higher' galeaspids ('Polybranchiaspidiformes' + Huananaspidiformes + Galeaspidiformes), it seems to retain a posterolaterally directed main lateral-line, a feature found with certainty only in *Hanyangaspis*, *Xiushuiaspis* and possibly *Dayongaspis*, thus, most probably a general galeaspid character.

CONCLUSION

Bannhuanaspis vukhuci is an unusually large galeaspid from the uppermost part of the Late Lochkovian to Early Pragian Si Ka Formation of Bac Bo (Vietnam). Its closest overall resemblance is with the 'Polybranchiaspidiformes' of the Early Devonian of China. However, it differs from all the genera classically included in the latter group by its transversely elongated median dorsal opening, laterally-placed orbits, and broad posterior shield margin with small cornual processes. *Bannhuanaspis* is more advanced than *Hanyangaspis*, *Xiushuiaspis* and *Dayongaspis* in possessing a single transverse commissural sensory-line. It shares with the Galeaspidiformes a posteriorly broad head shield with short cornual processes, and with the 'Polybranchiaspidiformes' and Huananaspidiformes a large number of gill openings. Its transversely elongated median dorsal opening, rather laterally placed orbits and posterolaterally directed main lateral-line are all generalized galeaspid characters.

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